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Forum

Persistence, multiple demographic strategies and conservation in long-lived Mediterranean plants

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Abstract. Persistence by longevity has been rarely considered as an alternative to regeneration by seeding for plants showing multiple demographic strategies. We propose a conceptual model of multiple demographic strategies for long-lived plants in stable habitats, shifting from regeneration by seeding to persistence by longevity and/or vegetative reproduction, along gradients of abiotic stress or interspecific competition. Regeneration by seeding would be promoted under low abiotic stress or under low competition, whereas persistence by longevity and/or vegetative reproduction would predominate at high levels of abiotic stress or competition. We test this model with two threatened species of the Mediterranean region, the shrub *Juniperus communis*, a widely distributed species which maintains relict populations in the Mediterranean mountains thanks to great adult longevity and *Pinguicula vallisneriifolia*, a palaeo-endemic herb relying on a perennial habit and vegetative reproduction under drought imposed stress or high competition at late successional phases. As a main consequence, multiple demographic strategies enhance a plant's ability to exploit environmental heterogeneity at different spatial (patches, localities, regions within the species' distribution area) and temporal (individual life span, glacial-interglacial cycles) scales. The potential of multiple demographic dynamics based on persistence and regeneration must be considered as a major ecological trait determining the long-term viability of peripheral populations of relict species as well as the inertia against extinction of many threatened endemisms, thereby contributing to the maintenance of the high plant diversity characterizing the Mediterranean region.

Keywords: Endemism; Environmental heterogeneity; Life-history strategy; Longevity; Peripheral population; Regeneration.

Introduction

The study of plant strategies is essential to understand both population and community dynamics. Strategies have been classified depending on plant responses to environmental gradients of productivity and abiotic stress, with vegetation patterns partially resulting from the co-occurrence of species with similar strategies (Grime 1979, 2001; Aerts & Chapin 2000). In addition to the differences in morphology and physiology, some authors have emphasized the consequences of life-history traits on plant co-existence, to understand how plant communities are shaped by interspecific differences in demographic dynamics (Grubb 1977; Bond & Midgley 2001; Grime 2001). In long-lived plants, both herbaceous and woody, a population maintenance trade-off has been suggested between *regeneration* (the replacement of individuals by seeding) and *persistence* (*in situ* maintenance of established individual plants) despite disturbances (Bellingham & Sparrow 2000; Bond & Midgley 2001). Thus, complementary to Grubb's (1977) 'regeneration niche', Bond & Midgley (2001) proposed a 'persistence niche' concept for a better understanding of the consequences of sprouting in disturbed environments. However, sprouting ability is not the only trait contributing to persistence, since many species remain established by great longevity (i.e. long life span by accumulated ageing or dead soma, or by vegetative body renewal conferring perpetual somatic youth; Harper 1977; Ehrlén & Lehtilä 2002), vegetative reproduction (e.g. clonality; Eriksson 1996) or a combination of the two (extreme ages in ancient trees may result from periodic coppicing; Rackham 1980). These traits could be especially significant in environments with low levels of disturbance, where complete losses of above-ground biomass are rare (Grime 2001), but also in nutrient-poor and/or abiotically harsh environments, where resprouting is prevented by resource limitation

(Bellingham & Sparrow 2000). Thus, typical examples of persistence by longevity and/or vegetative reproduction should be more frequent among stress-tolerant species inhabiting arid, alpine and tundra habitats (Grime 1979, 2001), as well as other poor but stable habitats such as cliffs and ravines (Larson et al. 1999, 2000).

The aforementioned interspecific trade-off between regeneration and persistence by resprouting has also been suggested at the intraspecific level, with members of the same species behaving mostly as seeders in resource-rich sites but acting as resprouters in resource-poor or climatically harsh sites (Enright & Lamont 1992; Kruger et al. 1997). These intraspecific trade-offs are, thus, reflected at the population level in the form of multiple demographic strategies, different dynamics of persistence or regeneration occurring in different environmental scenarios (see also Grime 2001; for the closely related term 'multiple regeneration strategies'). In addition, other traits promoting persistence, such as vegetative reproduction, have also been proposed to take part of multiple demographic strategies within single species, when occurring in environments characterized by low predictability of disturbance (see examples in Grime 2001). However, information about how longevity contributes to multiple demographic strategies and, more importantly, the environmental conditions promoting it is still lacking. Here, we present a conceptual framework implementing previous theories by considering plant longevity, together with vegetative reproduction, as major traits enabling persistence to be an alternative to regeneration across environmental gradients. Since multiple demographic strategies are the result of the interaction between species' genetic potential and the current environmental and management constraints, their identification and understanding might be a key issue for plant conservation in areas of high biodiversity. By illustrating our model with examples of threatened, long-lived plants in the Mediterranean area, we aim to highlight the importance of multiple demographic strategies for conservation.

A model of multiple demographic strategies

Assuming a low-disturbance environment, where important biomass losses by factors such as fire or herbivory are rare, our model proposes a shifting balance from regeneration by seeding towards persistence by longevity and/or vegetative reproduction along gradients of increasing unfavourability for sexual reproduction (Fig. 1). We suggest two different gradients: (1) gradients of abiotic stress, mostly determined by factors changing in relation to altitude, topography or latitude and (2) gradients of biotic stress determined by interspecific competition, as in succession in open patches after sporadic disturbance, with a high proportion of unoccupied habitat (low competition level) at the beginning but a low proportion (high competition level) at the end. Gradient axes would be orthogonal, indicating that the gradient of competition would be possible only in areas with low abiotic stress (see also Grime 1979, 2001), the range of existing environments being a triangular subset of the environmental space. Within this range, regeneration would be promoted under low abiotic stress and low competition, whereas persistence would prevail at higher levels of environmental stress or competition. The model might also reflect the relationship between stress and the spatial heterogeneity providing opportunities for seedling recruitment, high levels of stress representing low availability of microsites. We will test this model with the contrasting cases of *Juniperus communis*, a long-lived shrub, and *Pinguicula vallisneriifolia*, a perennial herb.

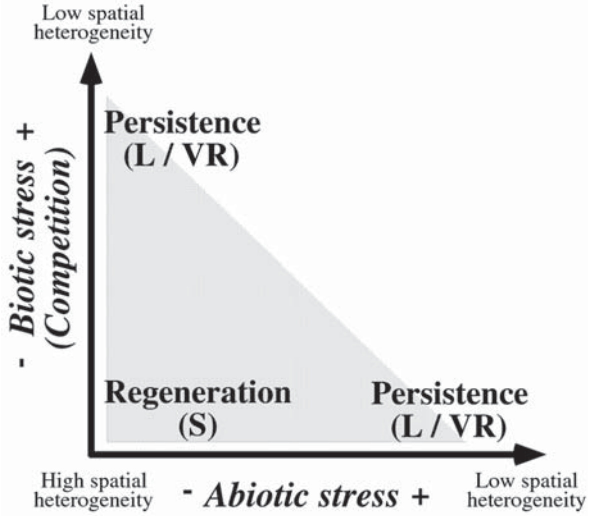

Fig. 1. Representation of multiple demographic strategies of persistence and regeneration and the traits promoting them (L = Longevity; VR = Vegetative reproduction; S = Seeding) shown by a long-lived species in relation to environmental gradients related to abiotic or biotic (competition) stress, at local or regional (distribution area) scales, under general low disturbance levels. The shaded triangular area indicates the range of existing environments as a subset of the environmental space. High levels of stress also involve low spatial heterogeneity (low availability of sites for seedling recruitment).

The common juniper *Juniperus communis* (*Cupressaceae*) is widespread across Europe and northern Asia but exists only as a relict from the last Ice Age in the Mediterranean mountains. It is a typical colonizing shrub ('seeder') in many parts of central and northern Europe (e.g. Faliński 1980). However, populations close to the species' distribution limit (such as those in Great Britain and the Mediterranean mountains of SE Spain) evidence a clear reproductive collapse, due to low production of viable seeds and high seedling mortality (Ward 1981; Clifton et al. 1997; García 2001; García et al. 1999, 2000). Abiotic stress associated with altitude (short growth period, low winter temperatures) and climate (severe summer drought) accounts for the regeneration bottleneck in the Mediterranean mountains. There, populations are currently dominated by adult and senescent individuals, with extremely low proportions of seedlings and juveniles (García et al. 1999). Seedling recruitment succeeds only in the few patches providing a wet substrate during summer, apparently being insufficient for the entire population to regenerate in a context of low spatial heterogeneity (García 2001; García et al. 1999). Thus, persistence in Mediterranean mountains is possible thanks to the remarkable survival ability and longevity of mature individuals, which in some cases can be as long as 1000 yr (Kallio et al. 1971). A contrasting regenerative pattern emerges among populations growing in continental Europe outside the Mediterranean region, where active recruitment by seeds is reflected in many seedlings and juveniles (García et al. 1999, 2000).

Pinguicula vallisneriifolia (*Lentibulariaceae*) is a palaeo-endemic carnivorous herb from SE Spain (Zamora 2002; Zamora et al. 1998). This plant inhabits moist limestone walls and cliffs, reproducing sexually by seeds and asexually by axillary buds and stolons. In addition, the perennating organ, a winter bud developing in late summer and from which a completely new rosette grows the next spring, allows persistence by longevity. Both sexual and vegetative reproductions depend on local resource availability (irradiance, prey abundance and water). However, these resources rarely occur in optimal combinations in the Mediterranean area, as sunny rocky sites with southern aspect are usually inhospitably dry, whereas wet rocky habitats are prohibitively shady (Zamora et al. 1998). As a result, different population dynamics take place in localities differing in the main aspect, or even in habitats within the same locality differing in small-scale topography. Populations living in moist, shady patches reproduce both sexually and asexually producing numerous seedlings and age-balanced populations. On the contrary, populations inhabiting dry, sunny rocky substrates, lack recruitment due to low seed production and poor seedling establishment caused by wet microsite scarcity. These populations are therefore dominated by adult vegetative (non-flowering) individuals persisting over time thanks to their perennial status in combination with asexual reproduction (Zamora 2002; Zamora et al. 1998). On the other hand, in some patches at the foot of the talus, abiotic conditions might become more favourable (i.e. more developed soil, relatively sunny and moist) and similar patterns of life-history variation occur along a gradient of interspecific competition by grasses colonizing these *Pinguicula* patches, after sporadic disturbance (e.g. rock crumbling). That is, seedlings are very abundant in areas with many open gaps, where plant competition is likely to be less intense (but see Bazzaz 1996), but almost absent from grass covered patches, where spatial heterogeneity is low and the population has a regressive structure dominated by vegetative adults (Zamora 2002).

Juniperus and *Pinguicula* have multiple demographic strategies involving persistence by longevity and/or vegetative reproduction and regeneration by seeding. In both species, seed production by adult plants decreased in high stress patches or sites, where senescent and vegetative individuals were dominant (García et al. 2000; Zamora 2002; Zamora et al. 1998), suggesting that multiple strategies could be, to some extent, the expression of trade-offs among life-history traits (Oostermeijer et al. 1994; Lesica & Shelly 1995). However, given that seedling recruitment is strongly limited by low spatial heterogeneity (microsite limitation) for both species, the demographic variation among persistence and regeneration might be also an epiphenomenon resulting from differential seedling and adult mortality, populations counterbalancing recruitment limitation thanks to adult longevity.

What are the ecological consequences of multiple demographic strategies?

The contrasting cases of *Juniperus* and *Pinguicula* illustrate how persistence and regeneration are alternative strategies used by the same species depending on the local or regional conditions. As a major ecological consequence, this demographic variability enhances the species' ability to exploit environmental heterogeneity at different spatio-temporal scales. At the local scale, plants are provided with a broad ecological spectrum, as a wide range of patches is efficiently occupied. Seeding represents a lottery in colonizing open, even distant, suitable patches whereas persistence ensures the permanence of the plant in an already colonized patch, even when the patch becomes unsuitable over time, due to succession (see also Oostermeijer et al. 1994; Colling et al. 2002). From a regional dynamic perspective, persistent populations might constitute a long-term seed source for a dynamic landscape of sink patches (Eriksson & Bremer 1993; Eriksson 1996; for clonal plants). At the geographical scale, wide distribution areas are allowed, since populations resort to persistence on the margins, where expansion, or even maintenance by regeneration, is precluded by climate. This is the case with *Juniperus*, considered to be one of the widest ranged gymnosperms (Vidakovic 1991); see also Grime (2001) for other plants relying on adult persistence at the limit of their distribution area). On a temporal scale, persistence implies that long-lived individuals contribute to the build-up of remnant populations, surviving long enough to bridge periods of unfavourable conditions and delaying the possible extinction process (Eriksson 1996; Ehrlén & Lehtilä 2002). In addition, adult individuals maintain long-term reproductive capabilities 'storing' recruitment potential to be deployed under sporadically favourable conditions, such as unusually rainy years (storage effect; *sensu* Warner & Chesson 1985). Finally, in terms of glacial-interglacial cycles, persistence would allow the existence of species 'refugia' from which populations recover during milder climatic periods (Bennett et al. 1991).

Implications for conservation and management

The identification of persistence as a main life-history strategy for plants, as well as the multiple demographic strategies involving persistence and regeneration, are relevant for species conservation. For example, persistence strategy seems to be crucial for the maintenance of distribution-peripheral populations, now considered to have high conservation value due to their role as reservoirs of genetic variability and potential for speciation (Lesica & Allendorf 1995). This seems to be the case of many remnant *Pinguicula* species, currently showing a highly scattered geographic range in southern Europe, and being the survivors of a species broadly distributed throughout the Mediterranean basin during the Quaternary (Zamora et al. 1996). Besides the genetic factor, persistent peripheral populations may play a keystone role, as is probably the case in *Juniperus* in the Mediterranean mountains, considered to be an umbrella species for herbaceous plants and invertebrate communities (many of them endemic, Molero et al. 1992; Blanca et al. 1998; see also Ward 1981). Finally, when located in areas free of human disturbance, such as high mountains or cliffs, peripheral populations might only be significant for species conservation at the scale of the distribution area, when core populations have been historically extirpated by anthropogenic pressure (Channell & Lomolino 2000).

Many plants now occurring as relict and endemic in the Mediterranean area are long-lived, stress-tolerant species inhabiting low disturbance habitats such as mountains and cliffs (Médail & Verlaque 1997). For them, persistence might be a significant strategy imposing biological inertia against extinction. In fact, the importance of adult longevity and survival for population persistence, compared to recruitment, has been evidenced for relict populations of Eurosiberian Pleistocene and Arctotertiary woody species (e.g. García et al. 1999; Hampe & Arroyo 2002), stenomediterranean species (e.g. Médail et al. 2002), palaeo-endemics from the Tertiary flora (e.g. García et al. 2002; Zamora et al. 1998; Picó & Riba 2002) and schizo-endemics which developed in the Mediterranean climate (e.g. Zamora et al. 1996; Albert et al. 2001). Therefore, persistence, as an important component of the diversity of life-history strategies, not only contributes to the preservation of the individual species, but also to the maintenance of the Mediterranean area biodiversity hot-spot, where high richness has resulted from the co-occurrence of species with different biogeographical and historic origins (Médail & Quézel 1997; Blanca et al. 1998).

Management of threatened species should consider the different potentials offered by the contrasting demographic dynamics. Thus, conservation efforts aimed to protect populations that rely on persistence should focus on the protection of established individuals against human disturbances such as clearing, burning or quarrying (Larson et al. 2000; Hampe & Arroyo 2002). On the other hand, in patches or localities where populations mostly reproduce by seeds, attention must be paid to processes controlling regeneration, emphasizing plant competition (Oostermeijer et al. 1994; Colling et al. 2002; Zamora 2002) and plant-animal interactions determining recruitment success, such as pollination, seed predation and seed dispersal (García 2001; Médail et al. 2002, Zamora 2002).

Concluding remarks

Regeneration and persistence may be considered as alternative pathways used by plants for avoiding extinction in the context of local or global anthropogenic impact. Longevity might decisively underlie the persistence pathway and, thus, contribute to the multiple demographic strategies promoting the adjustment of different populations of the same species to environmental conditions. The consideration of multiple demographic strategies as a major ecological trait in plants would enable us to: (1) interpret more accurately the patterns of abundance and distribution of species at ecological and geographical scales; (2) determine the ecological and historical causes of rarity, especially in areas of high biodiversity; (3) understand the filtering effect of human disturbance on vegetation, favouring species more resilient to disturbances (persistence by resprouting) against long-lived entrenched species (persistence by longevity) and (4) forecast plant responses to global change in regions of the planet with a long tradition of human impact, such as the Mediterranean area.

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